Rec. Queen Vict. Mus. II. 1. (15th July, 1947)

Some Notes on the Biology of the Cyrtidae (Diptera) with Special Reference to the Genus *Oncodes*

By

N. J. B. Plomley

Plates I-II

The Cyrtidae are a small family of dipterous insects whose larvae are endoparasites of spiders in all cases recorded. The flies are rare for the most part but under favourable local conditions may occasionally be found in large numbers. This applies especially to *Oncodes* and these notes record some observations on the biology of that genus, and, in particular, *Oncodes basalis* Walker.

Literature on Life-history of Cyrtidae

The literature on the life-history of the Cyrtidae consists essentially of records of the breeding of individuals either from larvae emerging from spiders or from pupae found associated with the remains of spiders; together with observations on the biology of the adults and oviposition, and descriptions of egg and first instar larva. The various records have been summarised from time to time, outstanding contributions being those of Cole (1919) and Millot (1938). Millot has dealt thoroughly with the development and biology of the Cyrtidae, in particular *Oncodes pallipes* Latreille, the larval and pupal stages of which he has described in detail.

Life-history records are available for only six genera, and may be summarised as follows:—

Acrocera

A. fasciata Wiedemann. Mature larvae and pupae in webs of *Amaurobius sylvestris;* notes on larva, with sketch (Emerton, 1890). Bred from ♂ ♀ *Lycosa stonei* Montgomery, one host having two parasitic larvae, the others one each; larvae emerged through abdomen; notes on behaviour of parasitised spiders (Montgomery, 1903; Johnson, 1903, 1904, 1915).

A. globulus Panzer. Parasite of a *Lycosa*; mature larva and pupa described (Nielsen, 1928, 1931). Bred from *Clubiona sp.* (Millot, 1938). Bred from *Lycosa spp.* (2 records), a Drassid and from an unknown spider (Locket, 1939).

A. sanguinea Latreille. Reared from cocoons of *Tegenaria agilis* (Brauer, (1883).

A. trigramma Loew. Reared from cocoons of *Tegenaria agilis* (Brauer, 1883).

Astomella

A. lindenii Erichson. Bred from *Cteniza ariana* Koch, the larva emerging through the abdomen; larval and pupal exuvia described and figured (Brauer, 1869). Further notes, with figures, on mature larva, which was found lying in the abdomen of the host with its spiracles in a lung book (Brauer, 1883).

Ocnaea

O. smithi Cole (m.s.). General account of life history illustrated by excellent photographs. Parasite of a trapdoor spider, California. (Jenks, 1938).

Oncodes

O. basalis Walker. Eggs laid on tips of twigs, so densely "that the buds died back and the twigs became quite black"; larvae progressed by leaping, curving the body like a bow (Froggatt, 1910, as *O. fumatus* Erichson). Bred from ♀ *Cosmophasis bitaeniata* Keys (Attidae), emerging from the abdomen; pupal period about 12 days (Dodd, 1906, as *O. doddi* Wandolleck).

O. brunneus Hutton. Eggs on twigs of apple and peach "which had apparently died back"; brief descriptions of egg and first instar larva; larva progresses by looping movements (Maskell, 1887; Anonymous, 1890).

O. costatus Loew. Pupal exuvium described (Malloch, 1915). Pupa figured (Malloch, 1917). Bred from *Lycosa sp.* (Kaston, 1937).

O. fuliginosus Erichson. Oviposition on *Equisetum limosum* (Stein, 1849).

O. fumatus Erichson. Pupa found in spider's nest (Brauer, 1869, quoting observations made by Gerstaecker).

O. gibbosus Linn. A parasite of *Prosthesima sp.* (Nielsen, 1931). A parasite of a Lycosid, possibly *Trochosa sp.* (Locket, 1939).

O. pallipes Latreille. Bred from a ♀ *Clubiona putris*, the larva emerging from the abdomen; larva pupated day after leaving host; pupal period a week; pupa figured (Menge, 1866; Brauer, 1883). Superficial description of pupa; host probably a *Clubiona* (Giard, 1894). Oviposition on ears of wheat; first instar larva briefly described (Marchal, 1899). Bred from a ♂ *Tarentula barbipes* Walck. (Lycosidae), the larva emerging through the abdomen; behaviour of parasitised host discussed (Locket, 1930; Bristowe, 1931). Eggs, larval stages and pupa described and their biology discussed in detail. Bred from *Aelurillus v. insignitus, Phlegra fasciata* and *Heliophanus sp.* (Millot, 1938). Parasite of *Lycosa pullata* and another Lycosid (Locket, 1939).

O. pallidipennis Loew. Bred from cell of *Sceliphron cementarius*, a spider-hunting wasp (Cole, 1919). Bred from *Pardosa banksi* and *P. suxatilis* (Kaston, 1937).

O. sex-maculatus Brunetti. 'Bred from a small spider at Serampore, near Calcutta' (Brunetti, 1926).

O. varius Latreille. Parasite of *Aelurillus insignitus* (Séguy, 1926).

O. zonatus Erichson. Bred from *Heliophanus sp.* (Millot, 1938).

O. fuliginosus Erichson/*O. zonatus* Erichson: Eggs laid on *Equisetum limosum*; notes on biology of adults (Gerstaecker, 1856). Larvae hatching from the eggs made wide leaps (Brauer, 1869).

O. gibbosus Linn./*O. zonatus* Erichson: Oviposition on dead twigs; eggs and first instar larva described and notes given on biology (König, 1894.)

Opsebius

O. diligens Osten-Sacken. Oviposition by captive females of 809 and 905 eggs, which hatched after 49 to 51 days; observations on biology of first instar larvae and adults (Cole, 1919).

O. agelenae Melander. Parasite of *Agelena naevia* (Melander, 1902).

Pterodontia

P. flavipes Gray. Mature larvae found in spider webs, the remains of spiders occurring near the larvae in two cases; larvae parasitised *Epeira serieata* in one case, and *Lycosa* (?) *pratensis* in five others; mature larva described; pupation day after leaving host and pupal period seven days; pupa described; observations on oviposition in the field; a captive female laid more than 2300 eggs in not longer than 45 minutes, and others 987, 3344 and 3977 eggs during oviposition; eggs described; incubation period 32-33 days; newly hatched larva described in detail and notes given on biology; spiders were infected experimentally and in one examined 17 days later 3 larvae were found in the abdomen and 27 in the cephalothorax and legs, of which latter 19 were above or near the ental opening of the coxae, the larvae being active and showing only slight distension of the body; in another examined 79 days after infection the larvae showed no change (King, 1916).

Miscellaneous

Collin (1919) considers a larva found in an egg-bag of *Epeira diadematа*, figured by Morley (1908), to belong to the Cyrtidae. Lindner (1936) refers to the biology of the family and structure of the first instar larva.

Biology of Adults

During collecting trips to Upper Blessington, Tasmania, in the summers of 1934 and 1938, *O. basalis* was observed in large numbers clinging, often in copula, to the tips of dead stems of sedges (*Juncus communis* and related forms) growing on the river flats of the North Esk River (Plate IIA). The flies were very sluggish, even in the hot sun, and were rarely seen on the wing. Their flight was very weak and they soon came to rest. The females were more sluggish than the males.

Oviposition

The eggs of *O. basalis* at Upper Blessington were laid usually on sedge stems, the dead tips being chosen for oviposition. This preference for the dead rather than the green stem was most striking and in only very few among thousands of cases were eggs found on green tissue. The dead stems occurred here and there among the green stems in the sedge clumps and appeared not to offer any advantage over the green stems. Usually the eggs covered the stems very densely, the layer being occasionally as much as 0.5 mm. thick (Plate I).

In the same locality eggs were found occasionally on grasses, on *Carex paniculata* (Cyperaceae), on *Xerotes longifolia* (Lillaceae), on *Eucalyptus sp.*, and on *Melaleuca sp.*, again invariably on dead stems and twigs. In other localities, in Tasmania and New South Wales, eggs of *Oncodes* have been found on dead twigs on *Eucalyptus spp.*, while the eggs of an English species, probably *O. gibbosus* Linn., were found at Cadnam, New Forest, in 1936, chiefly on dead grass stems and sometimes on dead tissue on gorse, conifer and sedge.

The stimulus involved in this preference for dead material for oviposition is not clear. With oviposition on sedge, the use of dead stems but not the green stems beside them, makes it unlikely that any factor of light and shade, shelter, accessibility or other positional effect was involved, as could well have been argued if oviposition had been found only on dead, and therefore leafless, twigs. The possibility that preference was given to dead tissue because of some surface quality was tested roughly in a field experiment using the English species. Four textures of surface were used, ranging from a highly-glazed ivory paper to a very coarse filter paper, all white or faint cream in colour. Sectors of these papers were glued to a circle of card placed in a petri dish, each paper occurring twice and in sequence. Flies were placed in the dish and laid a large number of eggs, but no preference was shown for any of the papers, eggs being deposited even on the glass of the lid. It may be noted also that at Upper Blessington large numbers of eggs of *O. basalis* were seen on the polished surface of a galvanised fencing wire. It seems unlikely therefore that the texture of the surface is the factor involved in oviposition on dead tissue.

The possibility that the dead sedge stems might be visited preferentially by spiders was also investigated. Numbers of stems were examined at night, the time the spiders were active, and it was found that both living and dead stems were visited indiscriminately. This was confirmed next morning by seeing everywhere threads of dewy web interlacing haphazardly on the clumps of sedge and other plants.

Oviposition probably occurs mainly in the heat of the day.

The First Instar Larva

Description

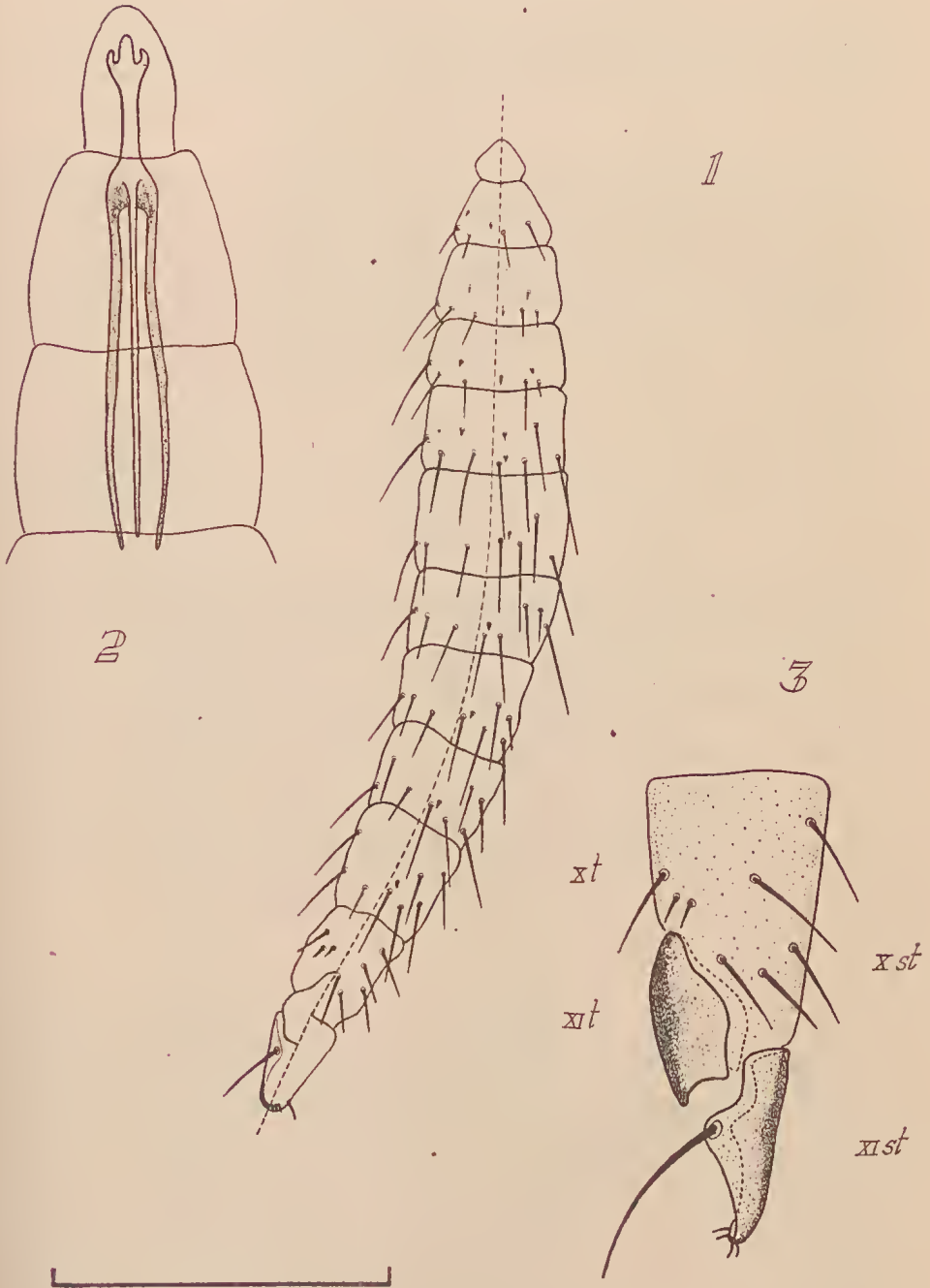
The first instar larva of *O. basalis* (Figs 1-3) closely resembles that of *O. pallipes* Latreille, described by Millot (1938); however, some discrepancies between his figures prevent exact comparison. Only minor differences in chaetotaxy occur and the buccopharyngeal skeleton of *O. basalis* (Fig. 2) appears to be the same as that of *O. pallipes*. The larva is about 0·3 mm. long, and more or less curved, the dorsal surface convex. The head is small. The body comprises 11 segments each of which bears setae. The setae are regularly arranged, those on the dorsal surface being almost constant in their arrangement from segment to segment. Some variation is found in chaetotaxy in a series of larvae.

In the head the pharyngeal skeleton comprises a rod, pointed anteriorly, and lateral processes; and behind the head, extending through the first two segments, three horns, two dorso-lateral and the other mid-ventral, which join the rod in the anterior part of the first segment. The head is apparently retractile, thus bringing about the extrusion of the tip of the rod and its processes. The pharyngeal skeleton in *O. basalis* appears identical with that of *O. pallipes* (Millot, 1938) (1).

The eleventh segment is modified as a springing organ (Fig. 3) by the development of anterior dorsal and posterior ventral boat-shaped sclerites which hinge into one another; the ventral sclerite bears two long bristles. The two sclerites are more heavily sclerotised than other parts of the larva and appear to be freely moveable about the hinge point, the complex of sclerites and bristles being concerned with the movements of the larva, particularly springing.

Millot (1938) states that the first instar larva of *O. pallipes* is metapneustic, the spiracles occurring dorsally on the last segment. Spiracles were doubtfully present, however, in the larva of *O. basalis*. Two clear areas were seen in the position shown

(1) Millot's figure 3 is stated to show the skeleton in dorsal view; it is apparently a ventral view.



FIGURES 1-3

Free-living first instar larva of *Oncodes basalis* Walker.

FIG. 1.—Larva showing chaetotaxy, dorso-lateral to left and ventro-lateral to right. Scale: 0·1 mm.
FIG. 2.—Head and segments 1 and 2, showing pharyngeal skeleton from below. Scale: 0·05 mm.
FIG. 3.—Segments 10 and 11, showing springing organ and bristles in side view, dorsal to left and ventral to right. Scale: 0·05 mm.

by Millot for the spiracles in *O. pallipes*, but these seem rather to result from an optical effect involving the hinge area between the dorsal and ventral sclerites. If spiracles are absent *O. basalis* will conform with the condition found in *Pterodontia flavipes*, which King (1916) found to be apneustic.

Conditions for Hatching

At Upper Blessington larvae of *O. basalis* were not found on the egg-covered sedge stems until late afternoon and apparently hatching did not take place to any extent until night. Larvae were therefore present on the stems during the period of activity of the spiders inhabiting the sedge clumps.

High humidity may be an important factor in hatching. In field experiments, when egg-covered stems were placed in jars at high humidity (RH = 100), numerous larvae were found after 1-2 hours, while in the controls only a few larvae were to be seen.

Movements

The free-living larva of *O. basalis* exhibited three types of movement. Firstly, there was a movement in which the larva bent, swayed or wormed this way and that, keeping the posterior end of the body fixed. In the bending movement the body flexed at the middle. Secondly, the larva progressed by looping movements; it stretched full out, grasped the surface and drew up the posterior end to the anterior. Thirdly, the larva could flip itself away. The anterior end was attached to the surface and the posterior end drawn up to it so that the larva was strongly curved. Simultaneous release of the two ends and straightening of the body (presumably accompanied by movement of springing bristles) flicked the larva a considerable distance. These observations agree with those of Froggatt (1910), König (1894), Bovey (1936) and Millot (1938), so that *Oncodes* differs from *Pterodontia* in the way in which the springing movement is brought about, in *Pterodontia* the larva standing erect and using only the springing bristles (King, 1916). Larvae in characteristic poses can be seen in Plate I.

The larvae will be distributed widely by these means and cases of infection of ground spiders will occur as well as the infections on the stems and twigs where larvae have hatched.

Infection of Host

On the egg-bearing stems the larvae seem to remain generally inactive, making only occasional movements. Vibration of the stem, however, results in a great increase in activity. That this activity is due merely to vibration and not to the presence of spiders was shown by several observations. A small spider was placed in a petri dish containing some *Oncodes* larvae and after running about for a few minutes had a number of them attached to it. As it became covered with the larvae, it tried to rid itself of them by shaking the chelicerae and cleaning the legs with the mouth parts; similar observations have been reported by Cole (1919). When the spider was still, no larvae became attached to it unless they wandered into contact with it. The larvae did not seek out the spider; for example, they were seen to wander close to it and then away again. The absence of any attraction of larvae to the spider is further shown by the attachment of larvae to insects (silverfish) placed in the petri dish with them. The silverfish were soon covered heavily with larvae. It may be noted that König (1894) records that larvae had been found attached to Podurids.

King (1916) concluded from the position of the parasites in the body of the spider that the larvae usually enter the host by penetrating the thin membranes at the articulations of the legs, while Millot (1938) suggests that larvae enter also through the body openings and particularly the lung books. In a laboratory infection of spiders by larvae of *O. basalis*, a larva was found half-way through the articular membrane between two segments of a palp.

All records published indicate that the first instar larva overwinters in the host. During field work at Upper Blessington a spider collected in a sedge tussock late in May, that is, at the beginning of winter, was found to be so infected.

As Millot (1938) and others have pointed out, the records show that there is no host-parasite specifity between Cyrtidae and spiders, at least in those few genera of which there is a knowledge of the life-history. Spiders are parasitised when by chance they come in contact with larvae, so that spiders whose habits are most likely to bring them into places where there are larvae are most likely to be infected. The habits of the free-living larvae are in accordance with this, as are the oviposition sites; large numbers of eggs are laid, with a corresponding high wastage of larvae. On the egg mass the larvae grasp on to any spider (as well as other organisms) coming in contact with them. Flipping off the egg mass and falling to the ground, they will be able to infect a wide variety of spiders which would not usually come in contact with them on the egg sites.

References

Anonymous. 1890.—Flies on apple twigs in New Zealand. *Insect Life*, 2, p. 288.

*Bovey, P., 1936.—Sur la ponte et la larve primaire d'*Oncodes pallipes* Latr. *Bull. Soc. Vaudoise Sci. Nat.*, 59, pp. 171-176, 6 fig.

Brauer, F., 1869.—Beitrag zur Biologie der Acroceriden. *Verh. Zool. Bot. Ges. Wien*, 19, pp. 737-740, pl. 13, f. 1-6.

————————, 1883.—Die Zweiflügler des kaiserlichen Museums zu Wien. III Systematische Studien auf Grundlage des Dipteren-Larven . . . *Denkschr. Akad. Wiss. Wien*, 47, p. 61, f. 89-92.

Bristowe, W. S., 1931.—Notes on the biology of spiders. VII. Flies that triumph over spiders. *Ann. Mag. Nat. Hist.*, (10), 8, pp. 473-474.

*————————, 1941.—*The comity of spiders*, 2, pp. 364-366, 540-541, f. 47. (London.)

Brunetti, E., 1926.—New and little-known Cyrtidae (Diptera). *Ann. Mag. Nat. Hist.*, (9), 18, pp. 561-606.

Cole, F. R., 1919.—The dipterous family Cyrtidae in North America. *Trans. Amer. Ent. Soc.*, 45, pp. 1-79, pls. 1-15.

Collin, J. E., 1909.—Note on the supposed larva of *Pimpla oculatoria*, F., figured in Morley's 'British Ichneumons', vol. 3, 1908, and its location among the Diptera. *Entomologist*, 42, pp. 97-98.

Dodd, F. P., 1906.—Notes upon some remarkable parasitic insects from North Queensland. *Trans Ent. Soc. Lond.*, for 1906, p. 124.

Emerton, J. H., 1890.—An internal dipterous parasite of spiders. *Psyche, Camb., Mass.*, 5, p. 404.

Froggatt, W. W., 1910.—*Proc. Linn. Soc. N.S.W.*, 35, p. 688.

Gerstaecker, C. E. A., 1856.—Beitrag zur Kenntniss der Henopier. *Stettin. Ent. Ztg.*, 17, pp. 339-361.

Giard, A., 1894.—Sur quelques parasites des araignées. *Bull. Soc. Ent. France*, (6), 14 pp. cliii-cliv.

Jenks, G. E., 1938.—Marvels of metamorphosis. *Nat. Geog. Mag.*, 74, (6), pp. 807-828.

Johnson, C. W., 1903.—*Ent. News*, 14, p. 64.

————————, 1904.—Some notes, and descriptions of four new Diptera. *Psyche, Camb., Mass.*, 11, pp. 17-18.

————————, 1915.—Notes on the species of the genus *Acrocera*. *Psyche, Camb., Mass.*, 22, pp. 198-203.

*Kaston, B. J., 1937.—Notes on dipterous parasites of spiders. *J.N.Y. Ent. Soc.*, 45, pp. 415-420, fig.

King, J. L., 1916.—Observations on the life history of *Pterodontia flavipes* Gray. (Diptera). *Ann. Ent. Soc. Amer.*, 9, pp. 309-321, pls. 15, 16.

Konig, A., 1894.—Ueber die Larve von *Ogcodes*. *Verh. Zool-bot. Ges. Wien*, 44, pp. 163-166, pl. 7.

Lindner, E., 1936.—Sack, P.—*Die Fliegen der palaearktischen Region*, no. 98, pp. 36, 3 pls.

* Papers so marked have not been seen by me.

LOCKET, G. H., 1930.—Note on the life-history of *Oncodes pallipes* Latr. (Dipt.). *Entomologist*, 63, p. 241.

————————, 1930.—Parasites of spiders. *Lond. Nat.*, for 1938, pp. 51-52.

LUNDBECK, W., 1907.—*Diptera Danica . . .*, 1, pp. 157-163.

MCCOOK, H. C., 1890.—*American spiders and their spinningwork*, 2, pp. 393. (Philadelphia.)

MALLOCH, J. R., 1915.—Some additional records of Chironomidae for Illinois and notes on other Illinois Diptera. *Bull. Ill. Lab. Nat. Hist.*, 11, pp. 341-342. pl. 81. f. 23.

————————, 1917.—A preliminary classification of Diptera, exclusive of Pupipara, based upon larval and pupal characters, with keys to imagines in certain families. Part 1. *Bull. Ill. Lab. Nat. Hist.*, 12, pp. 368-369. pl. 53, f. 1.

MARCHAL, P., 1899.—*Bull. Soc. Ent. Fr.*, for 1899, p. 286.

MASKELL, W. M., 1887.—On *Henops brunneus* Hutton. *Trans. N.Z. Inst.*, 20, pp. 106-108, pl. 10.

MELANDER, A. L., 1902.—Notes on the Acroceridae. *Ent. News*, 13, pp. 178-182.

*MENGE, F. A., 1866.—Preussiche Spinnen. *Schr. naturf. Ges. Danzig*, 1 n.f., (3-4), pp. 37-38.

MILLOT, J., 1938.—Le développement et la biologie larvaire des Oncodidés (= Cyrtides), diptères parasites d'araignées. *Bull. Soc. Zool. Fr.*, 63, pp. 162-181, 183-197.

MONTGOMERY, T. H., 1903.—Studies on the habits of spiders, particularly those of the mating period. *Proc. Acad. Nat. Sci. Philad.*, 55, p. 68.

*NIELSEN, E., 1928.—*De Danske Edderkoppers Biologi*, pp. 677-678, f. 460-462.

*————————, 1931.—*The biology of spiders*, pp. 220-221, f. 10.

SÉGUY, E., 1926.—Diptères (Brachycères) . . . Oncodidae . . . *Faune de France*, 13, pp. 157-168.

STEIN, F., 1849.—Dipterologisches. *Stettin. Ent. Ztg.*, 10, p. 118.

* Papers so marked have not been seen by me.

PLATES

PLATE I

Free-living 1st instar larvae of *Oncodes basalis* Walker on egg mass on sedge stem. The larvae can be seen in characteristic poses. The thread lines are spider web. Magnification about 30 x.

PLATE II

A. River flats at Upper Blessington, Tasmania with clumps of sedge and grasses. The tree line and rising ground at the back mark the course of the North Esk River.

B. Pupa of *Oncodes sp.* found under bark of *Eucalyptus sp.*, Narrabeen N.S.Wales. Note the web shelter of the host (torn away) and the threads, with droplets of fluid, suspending the pupa.